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Research Article

Will an ancient refuge become a modern one? A critical review on the conservation and research priorities for the red squirrel (*Sciurus vulgaris*) in the Iberian peninsula

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Abstract

Mediterranean peninsulas are well-known glacial refugia for several mammal species. For Eurasian red squirrel (*Sciurus vulgaris*), a forest-dwelling rodent, there is some evidence that population diversification was influenced by these refugia. Here, we review the poorly known history of the red squirrel in the Iberian Peninsula, and discuss current threats to this species, suggesting conservation guidelines and exploring several research lines for forthcoming studies.

Red squirrel populations suffered several bottlenecks in Iberia, but recently, after four centuries of absence, this species is expanding throughout the Portuguese territory. Although *S. vulgaris* taxonomic and genetic status needs further investigation, molecular data support the occurrence of a possible distinct cluster in the Iberian Peninsula. Additionally, a distinct and endemic population was recorded to the Sierra de Espuña, in Spain, which was probably the result of Quaternary climatic and vegetation fluctuations. Two major threats for red squirrels in Europe were identified: (i) habitat deterioration; and (ii) competition with the invasive Eastern grey squirrel (*S. carolinensis*). Conservation actions should focus on the conservation, restoration and appropriate management of suitable forested habitats. Although to date no grey squirrels occur in the wild in the Iberia, the trade and release of this invasive sciurid species is already forbidden by national conservation agencies in both Iberian countries and awareness campaigns are suggested.

An integrated research approach using both molecular and ecological data, and a large dataset containing samples from the entire Iberian Peninsula, should be followed to better understand historical, contemporary and future factors that may affect squirrel distribution.

A *refugium* is defined as "an area in which climate and vegetation type have remained relatively unchanged while areas surrounding it have changed markedly, and which has thus served as a refuge for species requiring the specific habitat it contains" (Lomolino et al., 2006). Climatic and vegetation fluctuations that occurred during the Pleistocene have shaped the distribution and population structure of several species (e.g. Haffer 1969; Hewitt 1996, 2000; Sommer and Nadachowski 2006). According to Refuge model of diversification, forest areas suffered an extensive fragmentation during Pliocene and Pleistocene, isolating populations in forested refuges, that later expanded their distribution ranges (Haffer, 1969). In the European context, Iberian, Italian and Balkan peninsulas are well-known refugia (e.g. Randi et al. 2004; Sommer and Nadachowski 2006; Grill et al. 2009; Sommer et al. 2009). Several mammal species have been restricted to these refugia during the Last Glacial Maximum, and later, during the Holocene, expanded their geographic distribution range to colonize central and northern Europe (Randi, 2007).

The Eurasian red squirrel, *Sciurus vulgaris* Linnaeus, 1758 (Rodentia, Siuridae), is a forest-living species and its distribution range is closely linked with the distribution of forests and woodland habitats (Lurz et al., 2005). Although phylogeographic studies on this widely distributed species are scarce (but see Hale et al. 2004; Grill et al. 2009; Dozières et al. 2012), there is evidence that red squirrels have rapidly expanded from a forested refuge in the Mediterranean region (Grill et al., 2009). In some Mediterranean areas, such as Calabria in South-Italy and Sierra Espuña in Southeast Spain, monomorphic and genetically distinct populations are reported (Grill et al., 2009; Lucas and Galián, 2009). The differentiation of these populations probably occurred during the Quaternary climatic and vegetation fluctuations as suggested by Valverde (1967) and Grill et al. (2009). For *S. v. meridionalis* from the Calabria region, Grill et al. (2009) stated that it forms an endemic evolutionary unit and a study combining genetic and morphological data is currently exploring the possibility that this unit may represent a distinct squirrel species (Wauters et al. *in prep*). For *S. v. hoffmanni* from the Sierra Espuña, Lucas and Galián (2009) suggested that this population should be considered as a management unit (MUs), defined by Moritz (1994) "as populations with significant divergence of allele frequencies at nuclear or mitochondrial loci, regardless of the phylogenetic distinctiveness of the alleles".

Here, we review the history of the Eurasian red squirrel in the Iberian Peninsula, considering distribution and taxonomic knowledge of this species. Additionally, we discuss current status and threats to red squirrels throughout Europe, mainly due to the presence of an invasive alien species, the Eastern grey squirrel (*S. carolinensis*). Fortunately, the Iberian Peninsula is still free from this invader; therefore, and aiming to maintain this scenario, we discuss conservation guidelines to the current and future maintenance of the red squirrel in the Iberian Peninsula. Furthermore, considering that little is known on the ecology of red squirrel in Iberia, we explore several research lines for forthcoming studies in order to provide an agenda to better understand historical,

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contemporary and future factors that may affect squirrel distribution and population size.

Brief history of the red squirrel in the Iberian Peninsula

Although present in central Europe since middle Pleistocene (Jánossy, 1986), the earliest red squirrel fossil record in Portugal dates from only 5000–6000 years ago, and was found in Cabeço de Arruda (Santarém, central Portugal, Telles-Antunes 1985). Red squirrel abundance and distribution in the Iberian Peninsula is virtually unknown until the Middle Ages. However, Telles-Antunes (1985) suggested that this species was probably widely distributed in Portugal from the Middle Ages until the 16th century.

During the 16th century, red squirrel populations suffered dramatic population declines, resulting in the extinction of the species in Portugal by the end of this century (Mathias and Gurnell, 1998). The combination of intense farming and tree logging for the naval industry, resulting in habitat destruction and fragmentation, have been suggested as the main causes for the decline and extinction of the red squirrel in Portugal (Petrucci-Fonseca and Mathias, 1987; Mathias and Gurnell, 1998). Similar declines in the 15th and 16th centuries have been reported for the British Isles, especially in Ireland, where red squirrel went extinct during this period and only recovered in early 19th century, when a series of reintroduction programs took place (Bosch and Lurz, 2012). Fast and wide-scale deforestation, resulting from agricultural clearings, sheep-grazing and iron-industry, was also the main cause of this decline in the British Isles (Bosch and Lurz, 2012).

Although the red squirrel was always present in Spain in the last centuries, this species also suffered range contractions in the Spanish territory (Telles-Antunes, 1985; Lucas and Galián, 2009). Lucas and Galián (2009) suggested that the red squirrel population in the Sierra Espuña went through a bottleneck, which might have occurred at the end of the 19th century, due to massive deforestation of this area. Bottleneck events are known to greatly reduce the genetic diversity (e.g. Allendorf and Luikart 2008), and red squirrel population in the Sierra Espuña is monomorphic for the control region of the mitochondrial DNA (Lucas and Galián, 2009). Local demographic collapses of red squirrel populations related to the 19th century massive deforestation were also recorded in the Italian Alps (Trizio et al., 2005). In more recent times, reforestation of these areas, increasing habitat connectivity, resulted in an increase in the numbers of red squirrels and in gene-flow between different populations (Trizio et al., 2005; Lucas and Galián, 2009). Currently, the red squirrel presents a discontinuous distribution in Spain (Fig. 1), being present in almost all forested areas with exception of the southwest region (Blanco, 1998; Purroy, 2002).

The recent expansion of the red squirrel into the Portuguese territory dates back only to the 1980s, when the first individuals were seen in the north of the country, near the border with Spain (Mathias and Gurnell, 1998). Large areas of pine woods became available through reforestation in northwest of the Iberian Peninsula, allowing the expansion of red squirrel from Galiza, Spain, to the north of Portugal (Mathias and Gurnell, 1998; Purroy, 2002). Such expansion was quite rapid, occurring within an area of 11700 km^2 from the Spanish border in the north and northeast of Portugal until the Douro River (Fig. 1) in about two decades (Ferreira et al., 2001; Purroy, 2002). Furthermore, occasional sightings were recorded in some areas southwards of the Douro River (e.g. Matos et al. 2007). This suggests that this species is currently expanding throughout the Portuguese country in landscapes with suitable habitat. Despite apparent good dispersal capabilities of red squirrels (e.g. Delin and Andrén 1999; Wauters et al. 2010), human activities, such as tree logging, road network expansion, hunting and wildfires may reduce habitat availability and suitability for this species.

Additionally, recent reintroductions took place in several sites in the Iberian Peninsula, especially in urban parks (Mathias and Gurnell, 1998; Purroy, 2002). Reintroductions are often considered as a conservation measure to increase the viability of endangered populations or to restore extinct populations (Bosch and Lurz, 2012) and studies in Belgium and Italy have defined clear guidelines for successful reintroduction of this species in both semi-natural and urban park habitats (Fornasari et al., 1997; Wauters et al., 1997a,b). Moreover, as red squirrels are attractive rodents, well accepted by humans, they are often used as a symbol for tourism (Bosch and Lurz, 2012). In Spain, reintroductions took place in the urban parks Retiro and Casa do Campo, Madrid (Purroy, 2002), and in Laujar de Andarax, Almería (Blanco, 1998). In Portugal, recent red squirrel reintroductions were also documented in urban parks: Parque Biológico de Gaia, Gaia; Jardim Botânico, Coimbra; and Parque Florestal de Monsanto, Lisboa (Mathias and Gurnell, 1998). Released individuals came from captive populations from other localities in the Iberian Peninsula, but, unfortunately, also from other European countries. In some cases, offspring of these non-Iberian squirrels dispersed and colonized neighboring areas (Palomares, 1988; Blanco, 1998; Mathias and Gurnell, 1998). As the genetic proximity with the local subspecies was not adequately considered in some of these reintroductions (e.g. Parque Biológico de Gaia), genetic admixture with local populations should be evaluated. Furthermore, the degree of success and/or failure of these reintroductions in the long term also needs proper evaluation.

Taxonomic status

Currently, two subspecies of red squirrel are recognized to the Iberian Peninsula (Lurz et al., 2005; Wilson and Reeder, 2005; Bosch and Lurz, 2012): *S. v. fuscoater* Altum, 1876; and *S. v. infuscatus* Cabrera, 1905, including its synonym *S. v. hoffmanni* Valverde, 1967. *Sciurus v. fuscoater* is common throughout Europe, and also occur in the most northern part of the Iberian Peninsula, including the Pyrenees, while *S. v. infuscatus* is restricted to the Iberian Peninsula (Mathias and Gurnell, 1998; Bosch and Lurz, 2012).

Grill et al. (2009) examined the genetic structure of *S. vulgaris* in Europe. Although mitochondrial data do not support geographical differentiation (with exception of a lineage, *S. v. meridionalis*, from Calabria, southern Italy), microsatellite data supported clusters congruent with their geographic localization (Grill et al., 2009). The Iberian group, which authors named *S. v. infuscatus*, was clearly differentiated from the remaining clusters (*S. v. fuscoater* and *S. v. meridionalis*). The authors argued that the difference between mutation rate of mtDNA and microsatellites could be one of the explanations for this discrepancy (Grill et al., 2009).

The recognition of red squirrel specimens from Sierra Espuña, in the southeast of the Iberian Peninsula, as a distinct subspecies, *S. v. hoffmanni*, dates to 1967 (Valverde, 1967; Lucas and Galián, 2009). Subsequent studies included this subspecies as a synonym of *S. v. infuscatus* (Lurz et al., 2005; Wilson and Reeder, 2005; Bosch and Lurz, 2012). Nonetheless, Lucas and Galián (2009) reported a single mitochondrial haplotype to the population of Sierra Espuña, which is not shared with the remaining analyzed populations. Apparently, this genetic differentiation corroborates previous analysis based on morphological and ecological aspects of specimens from Sierra Espuña (Valverde, 1967; Lucas and Galián, 2009). Furthermore, Lucas and Galián (2009) suggested that this population should be treated as a management unit.

A clear definition of *S. vulgaris* subspecies and evolutionary significant units or management units, based on both morphological and genetic tools, and on a large dataset containing specimens from localities throughout the entire Iberian Peninsula (but also in its remaining range), can trigger proper conservation steps to preserve the genetic pool of this species, its subspecies and some valuable populations.

Conservation, current threats and future strategies

The Eurasian red squirrel is found across most forested areas of Eurasia, and it is classified as Least Concern by International Union for the Conservation of Nature (IUCN) (Shar et al., 2008). Nonetheless, there have been well-documented population declines and range contractions in several countries (for review see Lurz et al. 2005; Shar et al. 2008; Bosch and Lurz 2012). Therefore red squirrel conservation status var-

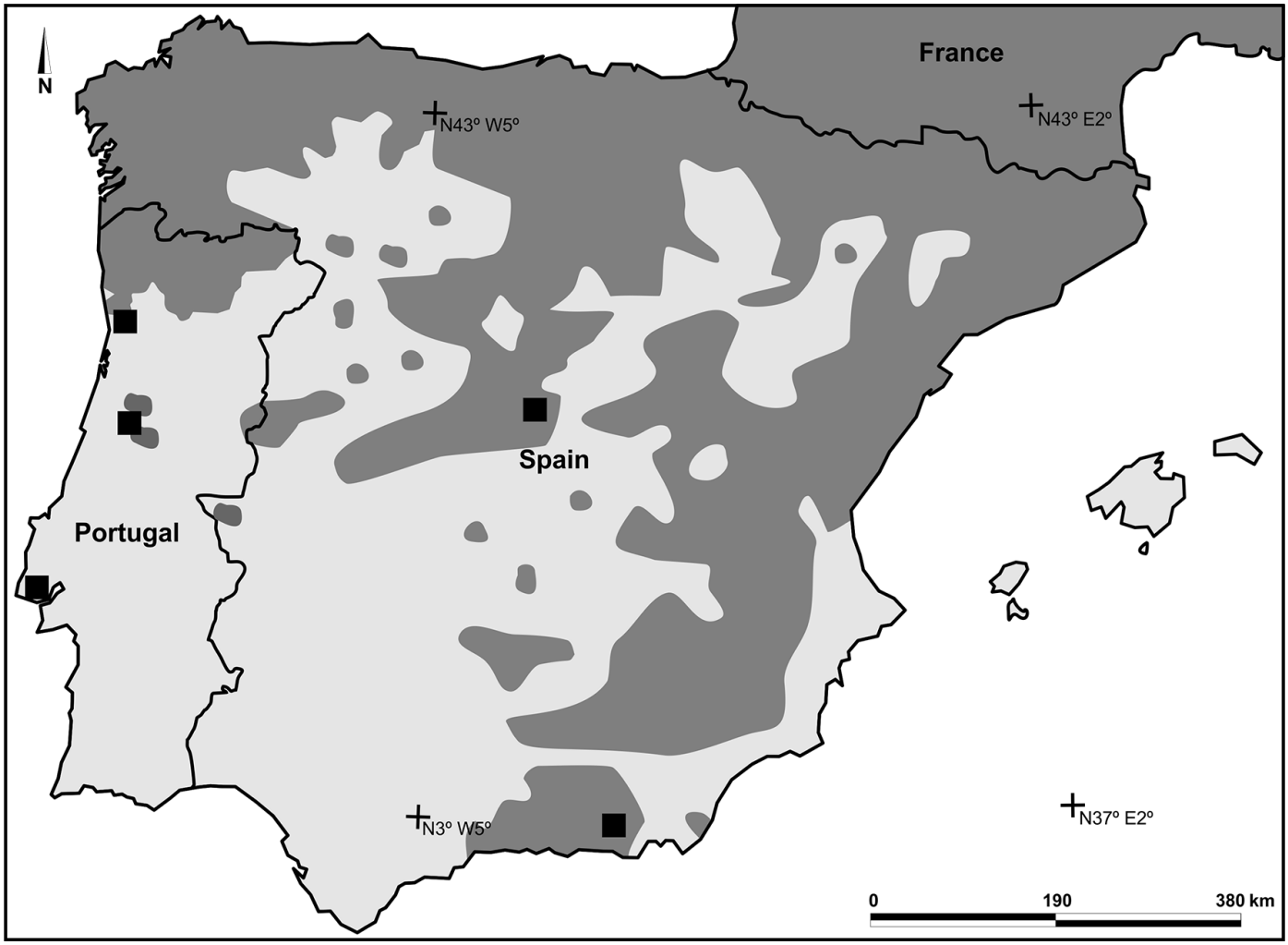

Figure 1 – Estimated distribution of the Eurasian red squirrel *Sciurus vulgaris* in the Iberian Peninsula. Geographic distribution data adapted from Ferreira et al. (2001) and Purroy (2002). Known reintroductions are shown in black squares.

ies according to regional and national laws, being under protection in countries such as Germany, Switzerland, France, Belgium, Italy and Great Britain (Bosch and Lurz, 2012). In the Iberian Peninsula, red squirrel is currently classified as Least Concern (Blanco and González, 1992; Cabral et al., 2005). Despite previously classified as Rare in Portugal, the recent range expansion of this species in the country supported the current classification (Cabral et al., 2005).

Major threats for red squirrel populations comprise habitat destruction and/or fragmentation and potential interspecific competition with introduced invasive tree squirrels (e.g. Bosch and Lurz 2012). As mentioned above, habitat loss and fragmentation have led to red squirrel population declines and consequent extinction in the Iberian Peninsula (Petrucci-Fonseca and Mathias, 1987; Mathias and Gurnell, 1998; Lucas and Galián, 2009), as well as in many other places within the range of the species (e.g. Wauters et al. 1994a,b; Koprowski 2005; Verbeylen et al. 2009; Rima et al. 2010). Nevertheless, red squirrels do occur in isolated urban parks, and in many fragmented habitats patchy populations thrive if seed production in woodland patches is sufficiently high and some degree of connectivity exists (e.g. Wauters et al. 1994a,b; Mathias and Gurnell 1998; Verbeylen et al. 2009; Wauters et al. 2010).

Currently, the increase of natural and human-induced fires in forests and the pine processionary moth (*Thaumetopoea pityocampa*), one of the main pine pests (Hódar et al., 2003; Arnaldo and Torres, 2005), are two important threats that can either cause direct habitat loss, or affect the viability of conifer forests reducing seed food supply to red squirrel populations in the Iberian Peninsula. The impact of pathogenic tree diseases on red squirrel conservation has been emphasized also in Great Britain (Shuttleworth et al., 2012). Appropriate forest management, with the creation of natural corridors and restoration of large forest areas (Gurnell and Pepper, 1993; Gurnell. et al., 2002), but also effective pest mitigation actions and fire control are essential to the conservation of this species in the Iberian Peninsula. Currently, national plans for protection against forest fire include prevention, surveillance, combat, and also restoring and rehabilitation of the ecosystems (e.g. Decreto-Lei n. 17/2009, Portugal), which are helpful to reduce the impact of this threat.

Additionally, interspecific competition with the invasive Eastern grey squirrel is currently a major threat to red squirrel in the British Isles and in parts of Northern Italy (e.g. Gurnell et al. 2004; Martinoli et al. 2010; Bosch and Lurz 2012; Bertolino et al. 2014). The grey squirrel is a very successful colonizer in European countries and tends to rapidly increase its range, having all the characteristics of an invasive species (e.g. Gurnell et al. 2001; Di Febbraro et al. 2013; Bertolino et al. 2014). Several authors have suggested that the ecological dominance of grey over native red squirrels is related to its higher body mass and more diverse foraging patterns, resulting in a more efficient exploitation of food resources, at least in mixed and broadleaved forests (Gurnell and Pepper, 1993; Kenward and Hodder, 1998; Wauters et al., 2001, 2002a,b). Moreover, in Great Britain, the grey squirrel is a healthy carrier of a squirrel poxvirus (SQPV) which causes disease in native red squirrel. The invasive squirrel is a reservoir host with, in general, no clinical signs of infection, but the virus is highly pathogenic in red squirrels, causing mortality in most cases (Rushton et al., 2000; Thomas et al., 2003; Tompkins et al., 2003). A juvenile red squirrel infected with poxvirus was recorded in the northeast of Spain; however this virus was different from UK poxvirus (Obon et al., 2011). This newly discovered poxvirus could represent a new emerging disease in red squirrel populations, which still has to be further studied to un-

derstand its relation with the one found in UK, and also to identify its prevalence in Iberian squirrel populations, since so far only one case has been recorded (Obon et al., 2011).

Contrarily to scenarios in Great Britain and Italy, where red squirrels are rapidly decreasing due to expansion of the introduced Eastern grey squirrel, in the Iberian Peninsula, where the congener is not present in the wild, red squirrel populations are expanding. However, it must be underlined that predictive models of expansion rates of the Eastern grey squirrel suggest that this species will expand throughout central Europe in the coming decades, unless severe management actions will be taken (Rushton et al., 1997; Lurz et al., 2001; Bertolino et al., 2008; Di Febbraro et al., 2013; Bertolino et al., 2014). Furthermore, although grey squirrel is not found in the wild in the Spanish territory, this species was already traded as pet and is catalogued as exotic invasive species in the Aragon Region (Real Decreto 1628/2011, Spain). In Portugal, there is no record of this species, but it is also mentioned in the list of exotic species, which constitute a list of species of high known ecological risk (Decreto-Lei n. 565/99, Portugal). Considering experience in Great Britain and Italy, once the Eastern grey squirrel is introduced, it becomes difficult or even impossible to control (e.g. Martinoli et al. 2010; Bosch and Lurz 2012; Bertolino et al. 2014), and effective control actions after introductions are often delayed due to logistic, legal, economic and social reasons (e.g. Bertolino 2008). Currently, the trade and release of these species is forbidden by national conservation agencies in both Iberian countries (Decreto-Lei n. 565/99, Portugal; Real Decreto 1628/2011, Spain). Additionally, awareness campaigns are also suggested to avoid grey squirrel releases, considering that in the past this species was already traded as pet in Spain (Real Decreto 1628/2011, Spain).

Identifying gaps and proposal of a new research agenda

Studies concerning Iberian squirrel populations have focused on some basic aspects of geographic distribution, genetic characterization, and taxonomic and conservation status, but only at a local scale (e.g. Valverde 1967; Palomares 1988; Mathias and Gurnell 1998; Ferreira et al. 2001; Purroy 2002; Moleón and Gil-Sánchez 2003; García and Mateos 2008; Lucas and Galián 2009; Talegón 2009). Some phylogeographic studies also included Iberian samples (Hale et al., 2004; Grill et al., 2009; Dozières et al., 2012), but only a proper sampling collection will better elucidate the evolutionary scenarios occurring in the Iberian Peninsula. Therefore, molecular tools should be used to uncover these events and to generate a genetic characterization at a fine-scale of the red squirrel in the Iberian Peninsula. Molecular markers with different evolution rates (e.g. mitochondrial DNA, nuclear introns and microsatellites) should be considered in order to clearly decouple historical and contemporary processes (Randi, 2007; Zellmer and Knowles, 2009; Wang, 2010). Additionally, a clear definition of subspecies and evolutionary significant units or management units within the Iberian Peninsula (but also in the rest of its range), using a multidisciplinary approach, will be useful to preserve the genetic pool of this species and that of specific populations with high conservation value.

Concerning the present situation of the red squirrel in the Iberian Peninsula, detailed studies on biology and ecology should be undertaken to increase the basic knowledge about this species and support its conservation. Field surveys should be conducted to investigate species distribution trends, and to identify environmental factors that may influence distribution and relative abundance. Additionally, integrated ecological studies should include ethology, veterinary, and trophic ecology to determine population viability. A systematic collection of roadkills can be easily organized and detailed post-mortem analysis including screening for known dangerous viral infections should be carried out (e.g. Everest et al. 2013; Romeo et al. 2013, 2014). Furthermore, conservation actions such as reintroductions and translocations must be carefully planned, using only founders of local and known genetic origin, in order to protect endemic populations (as those occurring in the Sierra Espuña). A monitoring plan, including screening for adenovirus (Everest et al., 2012), should be established to evaluate the degree of success and/or failure of these actions.

Ecological modelling has been widely applied to predict geographic distribution of suitable conditions (e.g. Gurnell. et al. 2002; Pearson et al. 2006). Available information on red squirrel distribution and environmental variables prone to affect this distribution can be used to create environmental niche models (e.g. Di Febbraro et al. 2013). This approach will help to define abiotic and biotic conditions within which squirrel populations can be sustained in the Iberian Peninsula. Additionally, simulations of future landscapes under climate and land use changes will help to anticipate detrimental effects of habitat loss and fragmentation on red squirrel populations. This information will be very useful to provide guidelines to promote priority conservation actions to allow the persistence of the red squirrel in Iberia.

Conclusions

The Iberian Peninsula represents the western limit of the geographic distribution of the Eurasian red squirrel (Shar et al., 2008). In spite of populations living at the edge of their species distribution being particularly susceptible to small variations in ecological factors (Romeo et al., 2010; Rodrigues et al., 2010), red squirrel populations in the Iberian Peninsula are currently expanding their range. Studying marginal populations can help to understand species responses to climate and habitat changes (Thomas et al., 2001). Therefore, filling knowledge gaps on red squirrel populations in the Iberian Peninsula by meeting the research agenda proposed in this review will not only help to uncover historical and contemporary patterns of these populations in the Iberia, but will also contribute to understand squirrel responses to future global changes. We attempted to highlight the need to direct public and scientific attention to regions that may become a stronghold for the Eurasian red squirrel, such as the Iberian Peninsula which was in the past a refuge for several mammal species. Such attention will help to avoid that alien squirrels can be introduced and that effective conservation measures to guarantee the survival of the Iberian native squirrel will be implemented.

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